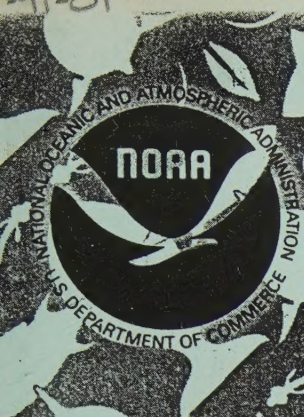
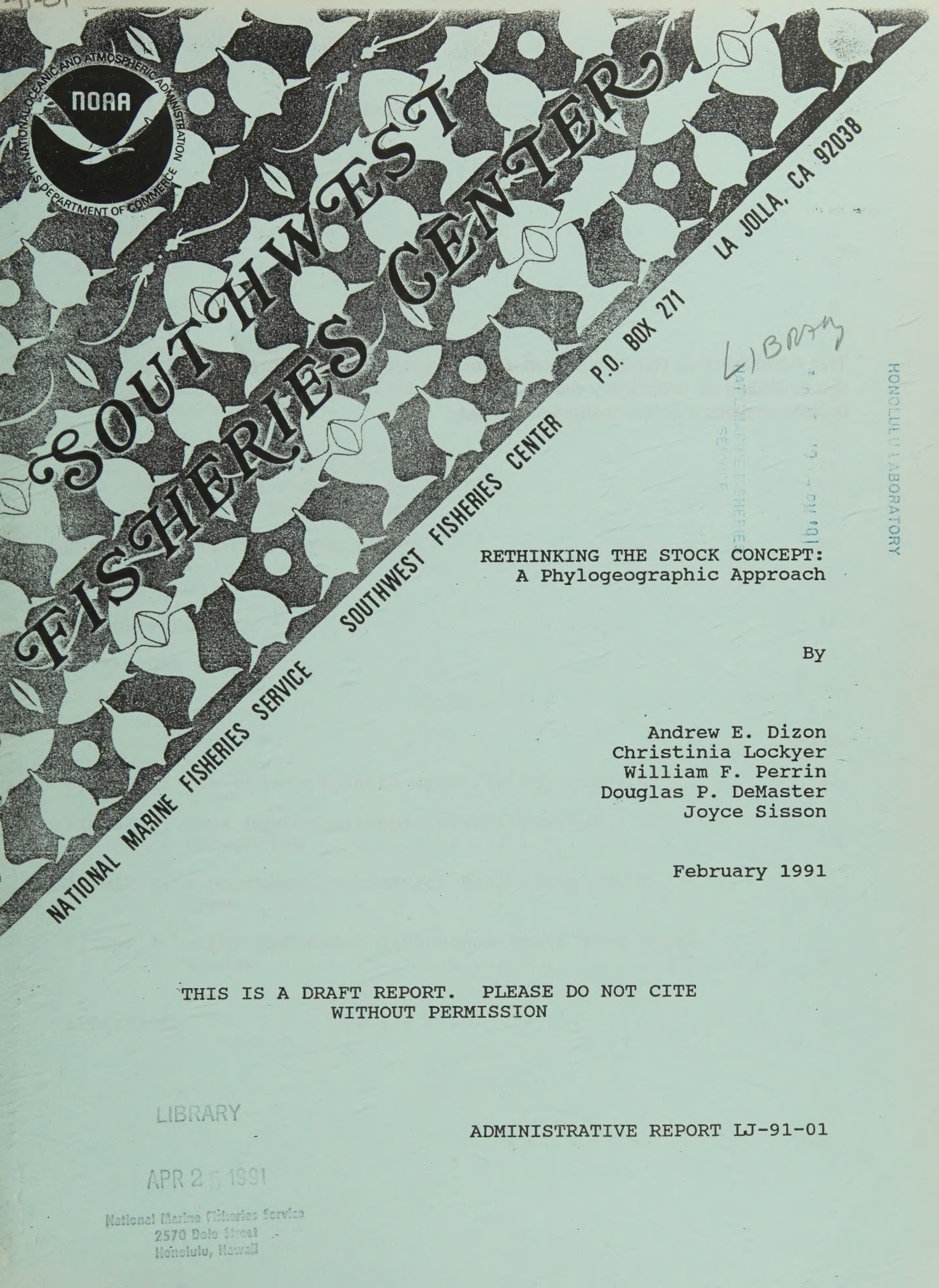




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RETHINKING THE STOCK CONCEPT:
A Phylogeographic Approach

By

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February 1991

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**Andrew E. Dizon, Christinia Lockyer, William F. Perrin,
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Abstract: In this manuscript, we review the various definitions of "stock" used to circumscribe a biological population for management purposes. Using marine mammal examples, we describe how the concept is central to two environmental acts by the U.S. Congress dealing with exploitable species and the management efforts flowing out of such legislation. We point out that no useful working definitions of stock are provided in the two Acts. We contend that the problem is more than semantic, and we offer suggestions and examples on how to classify populations so that the underlying biological structure is stated with the criteria used in the classification. That is, determination of a population's phylogeographic status ideally should be made before deciding whether it warrants management as a separate unit. By doing so, resource managers will be aided in making informed decisions on how to set priorities for management efforts and resources. Phylogeographic classification of populations also will help to focus research questions when investigating population structure and provide an interim solution for categorizing intraspecific divisions in situations where a complete set of data is not available.

INTRODUCTION

A "population stock," as defined in the Marine Mammal Protection Act of 1972 (MMPA), is a group of animals that share a common space and interbreed; a "vertebrate species," as defined in the Endangered Species Act of 1973 (ESA), is a distinct population segment that interbreeds. The intent of the use of such definitions in both Acts is to direct management efforts to taxon levels below that of the species to ensure that populations that are uniquely adapted to given areas are not irreversibly reduced by harvest or habitat destruction. Although the stock concept is thus codified into law by these environmental acts, no useful working definitions of intra-specific taxa are provided. At the same time, no universally accepted definitions or even any pro tem consensus exist among biologists. Thus, much confusion exists in the community of interest (researchers, regulators, users, and conservationists) as to what taxon levels conservation efforts are to be directed towards.

The problem with the definitions of stock in the Acts is that it is not obvious how to define quantitatively what is meant by either "sharing" or "interbreeding." For example, do we extend protection to the grey squirrels in Central Park in New York? They certainly meet the legislative criteria of sharing a common space and interbreeding. Or, for example, if members from two apparently distinct populations of dolphins only interbreed during El Niño events, does that mean these

populations should be managed as one management unit? What if their ranges overlap or they interbreed once every 100 years (or 1000 years)? Should they then be managed as separate stocks? Of course, there are no indisputable answers to these questions. It is absurd to apply a rigid, typological definition of stock in such situations, because now there are no means for determining how unique and isolated a population has to be before it is a "stock." Intraspecific structure theoretically can range from complete panmixia (no intraspecific structure) to a situation in which isolation has been so complete for so long that speciation processes are at work or almost complete (Fig. 1). Rather than striving for a universal definition that could be applied in the regulatory arena to decide if a population is or is not a "stock," what is required (and more practical) is to seek a means of describing the usually complex biological population structure in a more informative manner.

The purposes of this paper are to show that currently used and simplistic definitions of stocks are not very useful in satisfying management objectives and to propose how population structure could be described in a way that captures its complexity. Using examples from the marine mammal and fishery literature, we will review the history of the stock concept and methods used to infer stock structure. We will provide a suggestion on how to classify the various qualities

of stocks and conclude with a case study demonstrating how the suggested method can be applied.

BACKGROUND

Around the turn of the century, pioneering fishery biologists F. Heincke and J. Hjort established the local self-sustaining population as opposed to the typologically defined species as the preferred unit of study for fisheries management questions (see Sinclair 1988). Independently, Leopold (1933) recommended managing populations of wildlife based on their "radius of mobility," "rate of spread into unoccupied range," and "minimum units of range and population." This basic approach of managing a species at some sub-specific level has therefore been a tenet in resource management for almost 100 years. In general, stock status is conferred using a variety of proxies that imply reproductive isolation. With isolation comes genetic divergence through drift and through local adaptation via such processes as differential selection or character displacement. But, because reproductive barriers within species are fragile or incomplete, especially in the marine environment, the degree of isolation of one population relative to others can be complex, varying both in space and time.

One has to deal with a variety of other terms in the literature, all referring to organizational levels below the species: sub-species, race, deme, stock, and management unit.

The use of such terms in resource management literature is highly inconsistent. Only the term "subspecies" is recognized by the International Code of Zoological Nomenclature and is to be applied to populations where a trinomial name has been appended. The other terms, lacking such agreed usage, are frequently marshalled to describe a variety of populations for analytical convenience or to provide status to a group because it is the most conservative approach when data are lacking and conservation issues predominate. Many so-called stocks are mere "ecological abstractions" (Sinclair 1988), and what emerges from a perusal of the management literature is that when a term such as "stock" is used, it is used in the simplest and least restrictive sense. Little qualification is made or assumed about its genetic, evolutionary, or ecological implications. Misconceptions occur later when such stocks are expected to behave as if they were biological populations.

In 1980, an ambitious attempt at formalizing the stock concept was made with an international symposium (Stock Concept International Symposium convened at Alliston, Ontario, September 29 - October 9, 1980). Although there were many speakers who emphasized the importance of management by stock, in that very large symposium only one author ventured any formal definitions. Booke (1981) defined a "phenotypic stock" as any population that maintains characteristics that are expressed depending on the environment and a genotypic one as a population maintaining Hardy-Weinberg equilibrium, i.e.,

constant gene frequencies for a particular character in each generation. The phenotypic stock is similar to a later definition by Brown et al. (1987) as a population whose average life history parameters are meaningful from the standpoint of management. And the genotypic stock is similar to the definition of Larkin (1972), who described a stock as a population having a degree of genetic uniqueness: "a population of organisms which, sharing a common environment and participating in a common gene pool, is sufficiently discrete to warrant consideration as a self-perpetuating system which can be managed (p. 11)." Hoelzel and Dover (1989a) defined a genetic stock as one that is genetically differentiated. Presumably it is the population that Sinclair (1988) called the "local population" in his essay on population regulation and speciation.

The sense of this biological uniqueness is an evolutionary one, because it confers to the population a degree of fitness to local conditions and provides a reservoir of unique genetic variability. This is the "evolutionarily significant unit" (ESU) (Ryder 1986); it is a biological population that is distinguished by its presumed evolutionary uniqueness and significance. It is a natural unit and should be a better management unit than one that is not (Sinclair 1988).

Few would argue with this reasoning. However, determination of a stock based upon principles of adapted

genetic uniqueness conferring increased fitness is difficult to actually effect. Existing measures of fitness have little use in defining specific fitness to a local environment; experimentally it is an intractable problem for higher animals. As a result, typically stocks are defined using a variety of proxies that suggest this adapted genetic uniqueness.

STOCK CRITERIA

To study stock structure, an investigator makes observations of allopatry or isolation implying reproductive isolation, differential life history responses also implying reproductive isolation, morphological (i.e., protein structures) differentiation indicating drift or evolution under different selective regimes, or differentiation of neutral genetic characters quantifying the degree of isolation and the time since an ancestor was shared. We have categorized these sources of information as (a) distributional, (b) population response, (c) phenotypic, and (d) genotypic.

Distributional Data

Initially the most important item of knowledge is that of distribution and abundance. Data include all aspects of abundance, migration, pollutant and parasite loads, zones of fishery interaction and conflict, etc. that will provide information about the population movements relative to geographical space and time. This will largely define whether

there are major geographical barriers between putative stocks, and whether they are allopatric, parapatric or sympatric. Clearly, whenever there is a long-term barrier to mixing, the populations should be managed separately.

At the most basic level and without additional information, disjunct populations frequently have been designated as separate stocks for management purposes (Perrin et al. 1985). This is certainly a conservative approach. Even populations that overlap for portions of their life cycle may be disjunct stocks (Iles & Sinclair 1982). Overlapping distribution does not necessarily imply gene flow; natural processes favoring adaptation to local conditions, or social selection favoring maintenance of local social behaviors in the case of marine mammals, may serve to preserve genetic differentiation between putative stocks in the face of apparent overlap or movements between them (Ehrlich & Raven 1969; Slatkin 1987; Baker et al. 1990).

Presence/absence data on distribution are the most readily available sources of information on which to base stock identification decisions but are most easily misinterpreted. Sighting data from research platforms or catch data from fishery vessels, where search effort is not continuous, are very likely to cause discontinuities in the reported distribution of a species. In addition, a "snapshot" of distribution does not necessarily serve as a valid proxy for genetic or individual exchange rates because distributions

are rarely constant over time. On the other hand, for marine mammal species that are non-migratory and have a strong degree of fidelity to local areas (e.g., many coastal species), discontinuities in distribution alone may be adequate for identifying discrete populations.

Abundance information, i.e., where data on encounter rates and searching effort or data on catch rates and catch effort are available, provides a better proxy for exchange rates. Density "troughs" or large areas of zero density are indicative of allopatric populations. Yet once again, single snapshots of the density gradient may be misleading because of temporal variability in density. MacCall (1990) developed a model that describes how density, habitat variability, and movement patterns interact. Density dependent habitat selection is a key element in MacCall's model. The model suggests that as a core population's density is reduced relative to the density of neighboring populations, immigration to the favorable habitat increases. In addition, the variability associated with most estimates of density is such that the statistical power of using differences in density gradients in assigning stock status is often low.

Information on the movement patterns of individuals in a population brings one closer to properly assigning stock status to populations of marine mammals. Barriers to movement of individuals or gametes cause subdivisions to form within a population. These barriers may be recognizable based on

movement data. Reeb and Avise (1990) described evidence of concordance of genetic patterns with movements for a variety of species in response to biogeographic barriers. Information on movement patterns is thus one of the most reliable means for identifying barriers and evaluating the effects of management efforts. Effects of incidental or directed take on a population may be mitigated or exacerbated depending on where in the migratory cycle they occur. For most populations of marine mammals, research on movement patterns should be given high priority.

Population Response Data

The population response of the species is frequently modified by the environment. Here the demographic parameters, which may be different for various populations of the same species, are often influenced by density dependent control mechanisms. Data include all aspects of demography (age at sexual maturity, fecundity, growth rate and mortality), other biological parameters, social behavior, vocalization, and specific interactions peculiar to a particular population. The genetic baseline for the population may not be known, especially as these parameters can alter over time for the same group. There are very few data regarding the heritability of these responses even in the well-studied marine fishes (Bentzen et al. 1989), and we know of none in marine mammals. Furthermore, behavioral characteristics may also be modified by exploitation and intra- and inter-species competition,

affecting breeding site fidelity, nursing and care-giving to the young, and feeding habits with the associated pollutant and parasite loads. Our perception of the uniqueness of a population thus may be incorrect.

Still, there is an advantage to using population response criteria over abundance criteria that should be recognized: Samples taken at one point in time in the former integrate movement patterns over a much greater time scale than the latter does.

Differences in the timing of breeding provide a particularly valuable criterion, because a barrier to gene flow between populations is implied. Stock differentiation of spotted dolphins (Stenella attenuata) in the eastern tropical Pacific, although originally based entirely on distribution and morphology (Perrin et al. 1979), later was supported by differences in reproductive parameters (Barlow 1984, 1985). Barlow (1984) also could show differences in reproductive seasonality for northern whitebelly and eastern spinner dolphins (S. longirostris).

Differences in behavior have also been used to assign stock status. Davis and Lidecker (1975) supported the classification of the southern sea otter (Enhydra lutra) as a subspecies based on differences in hauling-out behavior between the Alaskan and Californian populations of otters. Vocalization behavior has been used to infer stock status between populations of Weddell seals (Leptonychotes weddelli;

Thomas & Stirling 1983) and between populations of north Pacific humpback whales (Megaptera novaeangliae; Yamamoto et al. 1989).

Phenotypic Data

The concept of self-sustaining stocks was formulated by Heincke through his extensive examination of discontinuous geographic variation of Atlantic herring morphology (Sinclair 1988). Stocks have been defined by morphological differences of every type; color patterns, body size, shape, and skeletal characters are some examples¹. For homeotherms, morphological characters probably represent underlying genetic code, and analyses of DNA and morphology should provide similar evidence regarding phylogenetic structuring of lower taxa levels (Sytsma 1990). The relative morphological differences between populations can be assumed to be a record of past (or present) differences in selection pressures or genetic drift. However, there are instances where morphological and molecular evidence differ due to either methodological or actual biological problems (see Box 1, Sytsma 1990). For instance, differential migration between sexes might produce strong mtDNA differences but little difference in chromosomal markers if males stray between populations and females do not. Some morphological

¹ The proteins examined electrophoretically are phenotypic expressions of genetic codes. However, such analyses will be included under genetics because traditionally such analyses have been considered as genetic and because such studies have also provided direct assessments of the genetic Hardy-Weinberg ratios in populations.

patterns, possibly color patterns or size differences, may be ecophenotypic, i.e., not stable to environmental variation. However, differences in morphological characters in marine mammals probably yield the clearest information regarding population uniqueness; because the variation is assumed to be both adaptive and heritable, it is a record of past selection pressures. Given adequate sampling, morphological differences between one or more populations strongly suggest limited gene flow among these populations either due to extrinsic barriers or selection. As in the case of the population response criteria, these types of phenotypic data also integrate movement patterns over a much larger time scale than do abundance data.

Evidence of morphological differentiation has been the predominant means for assigning stock structure to marine mammal populations. For example, Perrin et al. (1985) have documented population-specific differences for spinner, spotted, and common dolphins (Delphinus delphis) in the eastern tropical Pacific, and those populations have been afforded stock status and mortality quotas applied to the take by U.S. tuna purse-seiners (Anonymous 1987). Roest (1976), and more recently Wilson et al. (1990), used skull morphology to separate sea otters from Alaskan and Californian waters into separate stocks subsequently used as management units.

Genotypic Data

Booke (1981) defines a genotypic stock as a population maintaining Hardy-Weinberg equilibrium; presumably, it can be defined as any population that shows fixed genetic or temporally stable gene frequency differences when compared to other populations. Data include all studies that involve the analysis of some part of the genotype. The studies can be classified into the familiar allozyme studies, where electrophoretically detected alleles behave essentially as neutral markers, and the more recent DNA studies, where nucleotide sequence is determined. Genetic studies have been conducted via gene purification and sequencing (see Kocher et al. 1989 for recent references), thermal renaturation (Brown et al. 1979), restriction enzyme digestions of both mitochondrial and nuclear sequences (see Hallerman & Beckmann 1988; Harrison 1989 for recent references), and DNA fingerprinting (Pemberton & Amos 1989) and have been used successfully to study within- and among-population genetic differentiation. The techniques involved in genetic studies and their application to marine mammals have been reviewed recently by Hoelzel and Dover (1989a) and have been the subject of a recent International Whaling Commission workshop.²

² Authors note to reviewers: The proceedings of the workshop are currently in press. References to IWC Doc. SC/S89/GEN in the citation section are to manuscripts that were submitted to that workshop. We anticipate that they will be published in the proceedings volume prior to publication of this manuscript. Citations will be updated when available.

The evidence obtained from genetic methods is considered by resource managers as the most unequivocal for differentiating species and their intra-specific structure. However, there are problems in using genetic information for management purposes. Clearly it could be the ideal tool if we could directly examine the genes that constitute the locally adapted genome. One can not do this and must rely on the analysis of neutral genes, primarily using allozymes and mtDNA, that are assumed mostly independent of selective forces. If this can be assumed, the degree of genetic divergence between two populations is a measure of the relative time since they shared a common ancestor. While we believe that significant morphological differences usually represent adaptive evolution in disparate environments, mtDNA differences between two populations may simply be a measure of time of separation. Through rapid evolution through drift, significant mtDNA differences could accumulate in different allopatric populations that inhabit similar environments. Still, none of these populations would presumably harbor unique adaptive genetic variability and would perhaps not warrant separate management status. In the opposite situation, lack of significant mtDNA differentiation between two populations may not speak against separate stock status. Where barriers are "leaky," mtDNA genomes can rapidly penetrate neighboring populations independently of the chromosomal genome (Ferris et al. 1983). These "foreign" mtDNA genomes are

not selectively removed from the population--they are presumably neutral. The appearance of these foreign genomes argues for "homogenizing" gene flow and lumping the populations as one stock. In actuality, significant variation between the population still may develop in the chromosomal genome due to differential selection pressures. As an extreme example, in Lake Victoria, 14 morphological species representing 9 genera of cichlids show almost no differentiation in mtDNA sequences that are 803 base pairs in length (Meyer et al. 1990). In this case mtDNA would be a poor proxy for demonstrating differences in adaptable variation between population.

In the past when significant gene frequency differences between two putative populations were not found, it was easy to pass off the result as a negative one (i.e., the test was insufficiently sensitive because not enough samples or polymorphic loci were tested). And when significant gene frequency differences were detected among populations, the resource biologists have probably known from a variety of other criteria that gene flow among the groups was highly restricted. This was because considerable time and isolation were required to generate detectable differences, i.e., no more than a few individuals per generation. Thus differentiation in a genetic marker has been taken by resource managers as unequivocal evidence of stock discreteness, because they operate with the mind set that populations should

be divided into separate units when interchange rates are only several percent per year.

However, sequencing progressively longer segments of the mtDNA and nuclear genome now offers means of detecting genetic differentiation in the face of exchange rates that may be considerably higher than a few genomes per generation. So the question now must be asked, at what level does a population become "pan-mixed"? Deciding this requires an understanding of how much gene flow and consequent genetic diversity is "significant" or not.

PHYLOGEOGRAPHIC TAXA

Clearly the complex interactions among movement, introgression, selection of nuclear and cytoplasmic genomes and the variability of expression of those genomes between local populations of a species, result in situations that are not conducive to a simplistic definition of stock or a binomial decision of stock or not-stock. Deciding whether a putative local population should be managed as a separate unit requires considerable expert biological judgement. As long as there are no means of routinely measuring the total genetic variability of local adaptation, rather than its proxies (distribution, population responses, phenotypic variation or neutral genotypic variation) subjective decisions are necessary.

For other purposes, Avise et al. (1987; Avise 1989) devised a framework with which to organize hypothetical population structures and with which to relate the two critical concepts of selection and movement or their products--phylogeny and distribution. They first proposed five categories but later reduced them to four (Avise 1989), two with discontinuous genetic patterns and two with continuous ones. The approach classified assemblages into one of four categories based on two criteria: mtDNA genetic distance and spatial distribution. We changed their criteria slightly; in our scheme, the horizontal axis indicates the degree of differential selection likely to have occurred in one population relative to another. It represents differences in characters that are the expression of the locally adapted genome rather than simply the mtDNA genetic distance (Fig. 2). Under this scheme, differences found in demographic, morphological, isozyme, or mtDNA measures are taken to be proxies indicating that selection may be operating differentially on one population relative to another. Measures on this axis mostly represents the culmination of selection operating on many generations. Gene flow and its proxy, distribution difference, is the other axis of the matrix. It is considered separately to emphasize that available information usually only is indicative of potential gene flow. Actual flow of genes requires the production of fit offspring.

The advantage of looking at populations in this way is

that a hierarchy of four population relationships can be operationally described. It is a hierarchical relationship because with each step there is an increasing probability of the population in question being an ESU (Phylogeographic categories I through IV; Fig. 2). Note that in characterizing a single population for management purposes, it is always relative to another reference one. This is how the proposed system works.

Category I Populations

The easiest situation to deal with is allopatric populations demonstrating significant genetic differences; there would be little argument that these should be managed as separate units. Category I is characterized by a discontinuous genetic divergence pattern where locally adapted and closely related genome assemblages are separated from other ones geographically and by significant genetic distances--great genetic divergence/strong geographic partitioning. This could have been caused by long-term, extrinsic barriers (zoogeographic) or extinction of intermediate assemblages in cases with limited gene flow.

Category I situations are characterized by the presence of actual geographical separation by physical barriers such as land masses, or oceanographic or topographical barriers such as temperature clines, etc., which effectively create a margin around a population. Genetic and other differences from populations elsewhere are implied but are not necessarily

proven. The population is effectively isolated and probably is never confused with another in management programs.

Category II Populations

Category II is similarly characterized by a discontinuous genetic diversity pattern between groups of closely related genome assemblages existing sympatrically or parapatrically--great genetic divergence/weak geographic partitioning. Avise et al. (1987) speculate that this may have arisen through allopatric divergence and secondary contact or some intrinsic (reproductive) barriers.

This requires that two (or more) populations/putative stocks actually co-exist with total sympatry, with extensive geographical overlap, or weakly defined in parapatry. Geographically there would appear to be no reason not to manage them together, but critical differences in behavior, morphology, genetics, or some combination of these have resulted in reproductive isolation to some degree. This type of stock is perhaps the most critical and difficult in management.

Avise et al. (1987) and Avise (1989) find no good examples of this category and report that it is rare to find mtDNA differences greater than 1% to 2% between individuals collected from the same locality. Using mtDNA divergence measurements, Hoelzel (1989) reports considerable genetic isolation between sympatric populations of killer whales (Orca

orcinus) off Vancouver Island; they suggest that these groups represent a category II population structure.

Category III Populations

The other two categories are characterized by a continuous genetic divergence pattern. Category III parallels that of category I; however, here the geographically separated assemblages are characterized by little genetic differentiation; for instance, less than 1% for mtDNA diversity. Still, populations are clearly separate, either because of true allopatry or strict parapatry, and there is a high degree of reproductive isolation, although there are no barriers to intermingling at the margins, and interbreeding is feasible. There may or may not be various combinations of demographic, morphological and genetic differences. Nevertheless, geographically concordant unique genome assemblages develop within local habitats.

Category IV Populations

Category IV populations have extensive gene interchange and no subdivision by geographic barriers. Populations in this category appear panmictic and occupy a broad range that blends with that of neighboring population(s) rather than abuts on them. There are usually minimal, if any, differences in morphology, genetics, and demographic parameters between them, and the main distinguishing feature that this is a separate population is that the center of abundance may be some distance from the center of neighbors. There is little or no

reproductive isolation, and there is considerable intermingling on breeding grounds. This category typifies the most nebulous classification and may show poor evidence for any stock differentiation. Depending on the management issue, certain geographical regions occupied by such population(s) may still be treated as separate stocks for the sake of conservatism.

QUALIFIED PHYLOGEOGRAPHIC TAXA

The manner in which such a phylogeographic classification of any given population is made and the confidence in such a decision depends on the amount of information available. We suggest that this information be appended to the phylogeographic taxa in a shorthand method (Fig. 3). A shorthand notation is necessary because resource management documents usually contain extensive lists of stocks that are or are being considered for separate management status. Using this approach, reference to a given management unit would carry with it information regarding its phylogeographic structure (category type) and the data from which the decision was made (criteria basis).

The phylogeographic category is designated by the Roman numeral (I, II, III, and IV; Fig. 2). The proxy information with which decisions regarding the population is made is designated as "a" (distribution and movement), "b" (population responses), "c" (phenotypic differences), and "d" (genotypic

differences). A population would be designated by phylogeographic category and decision criteria, e.g., II a/bcd. Letters to the left of the solidus would represent data for "lumping" and those to the right, data for "splitting" the group (fig. 3).

A population that has a high probability of being an ESU is immediately apparent from its phylogeographic category. The degree of confidence in such a classification is indicated from the type of information that was marshalled to make the decision. Situations where information was lacking or equivocal could be informative from a management sense. In cases where information regarding one or more of the criteria were unavailable, the letter designation would not be present (perhaps a dash could be substituted), or the same letter could appear on both sides of the solidus if information was equivocal or unresolvably contradictory. A stock designated as a type IIIc/ad probably would stimulate more aggressive management than one designated type IIIc/a, plus it would help focus additional research efforts. In the situation where there is clear geographic separation but extensive overlap of margins temporally, as in III type stock, we might wish to denote this fact by indicating the stock as IIIa/a. In another example, where population response is to be included in the stock category, there might be no difference between demographic parameters, pollutant, and parasite loads, but clear differentiation between dialects. The stock that perhaps

might be type II might then be designated as IIb/b. If all aspects showed clear differences, then the category would be II /b.

In the appendix, we have chosen a species to illustrate the procedure. The minke whale (Balaenoptera acutorostrata), whose complex intra-specific structuring has populations with relationships demonstrating each of the four phylogeographic categories. Current biological information on the minke whales is described in detail, covering as much ground as possible under each of the four criteria. Then, classifications are suggested for the various putative stocks.

THE DECISION PROCESS

This proposed system of phylogenetic classification of course addresses only single-species considerations. Because of ecological phenomena such as predator-prey interactions, the existence of keystone species and species guilds, etc., a population may have importance beyond its qualifications, or lack thereof, as an ESU; these factors must also be considered in deciding what should comprise a management unit.

It is most important that the phylogenetic classification be carried out as an exercise separate from and prior to consideration of the socioeconomic and political factors that inevitably influence the management status of a population, and, further, potential conflicts of interest should be carefully weighed and considered in selection of an expert or

panel of experts to make the classification. Ideally, populations would be surveyed and phylogeographically classified before situations demanding management decisions arose.

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FIGURES

Fig. 1. Two views of intra-specific structure, a "typological" and a "biological" conception of populations within species. The circles, labeled with lower case letters, are individual populations whose geographical habitat is represented by its size and position within the species space. Where circles intersect, habitat is shared. The arrows represent exchange rates: infinitesimal between species, variable between populations within species.

In the first view, individual populations within a species are perceived as isolated, allopatric entities that can be uniquely described. Interchange between the populations, while greater than between species, is still very low, i.e., on the order of a few genomes per generation.

In the second view, the complexity and wide range of potential intra-specific structures are recognized. Habitats range from completely separate to situations where one is completely within another. Exchange rates vary between various populations, in some cases with great temporal variability due to environmental and population density changes.

TWO VIEWS OF INTRA-SPECIFIC STRUCTURE

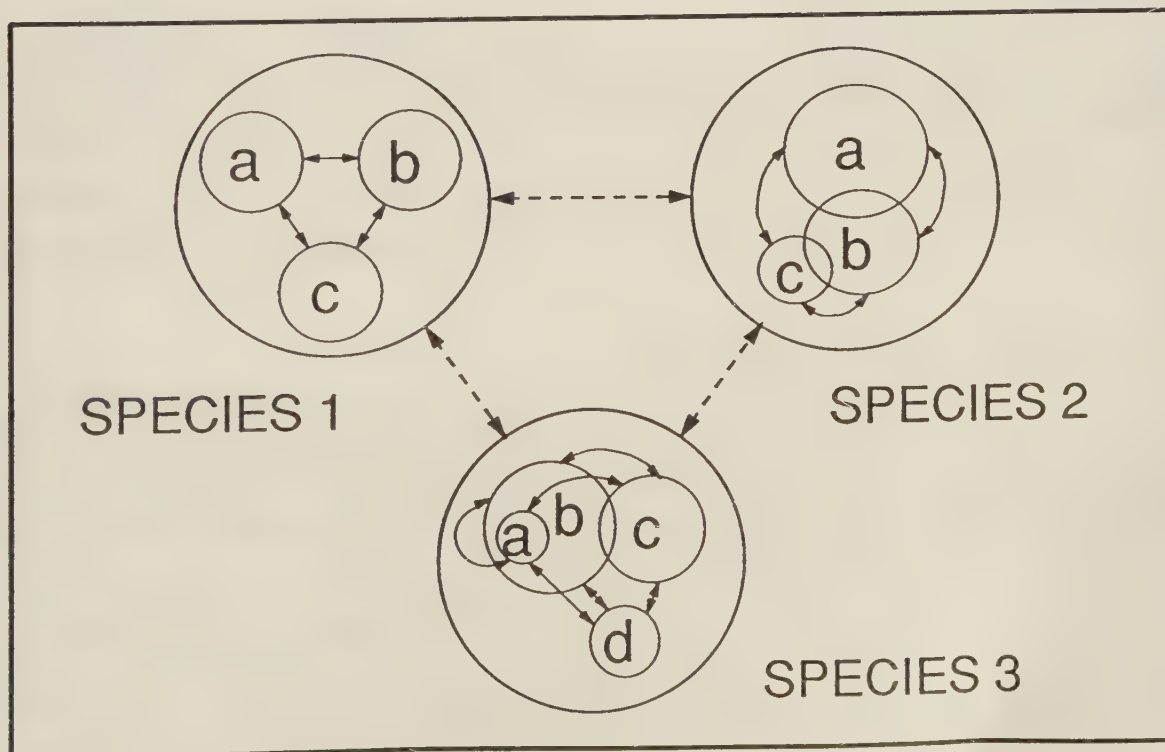
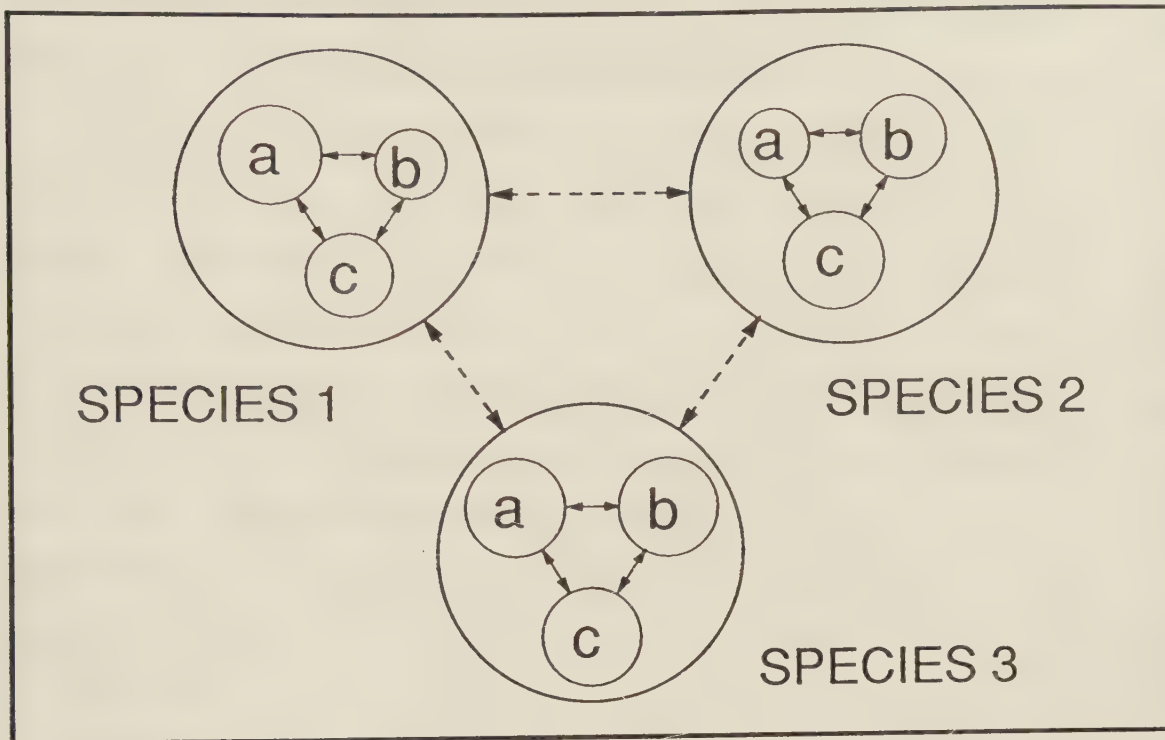


Fig. 2. Four phylogeographic classification categories. The horizontal axes in the theoretical classification refers to differences in the characters expressed by the genes that make up the locally adapted genome. The horizontal axis in the operational classification refers to differences in characters that may or may not be expressed by the genes that make up the locally adapted genome. If not, then the differences represent proxy measurements indicating the probability that sufficient time has elapsed and selection pressure has been applied so that a locally adapted genome has evolved. Gene flow is defined as production of locally fit offspring. Adapted from Avise 1989.

Theoretical Classification:

		PHYLOGEOGRAPHIC TYPES	
GENE FLOW	little or none	III	I
	high	IV	II
		little	great
		DIFFERENTIAL SELECTION	

Operational Classification:

		PHYLOGEOGRAPHIC TYPES	
GEOGRAPHIC LOCALIZATION	great	III	I
	little or none	IV	II
		little	great
		PROXIES for DIFFERENTIAL SELECTION	

Fig. 3. A shorthand method for qualifying stock type using phylogeographic categories and information regarding the criteria used to make such qualifications.

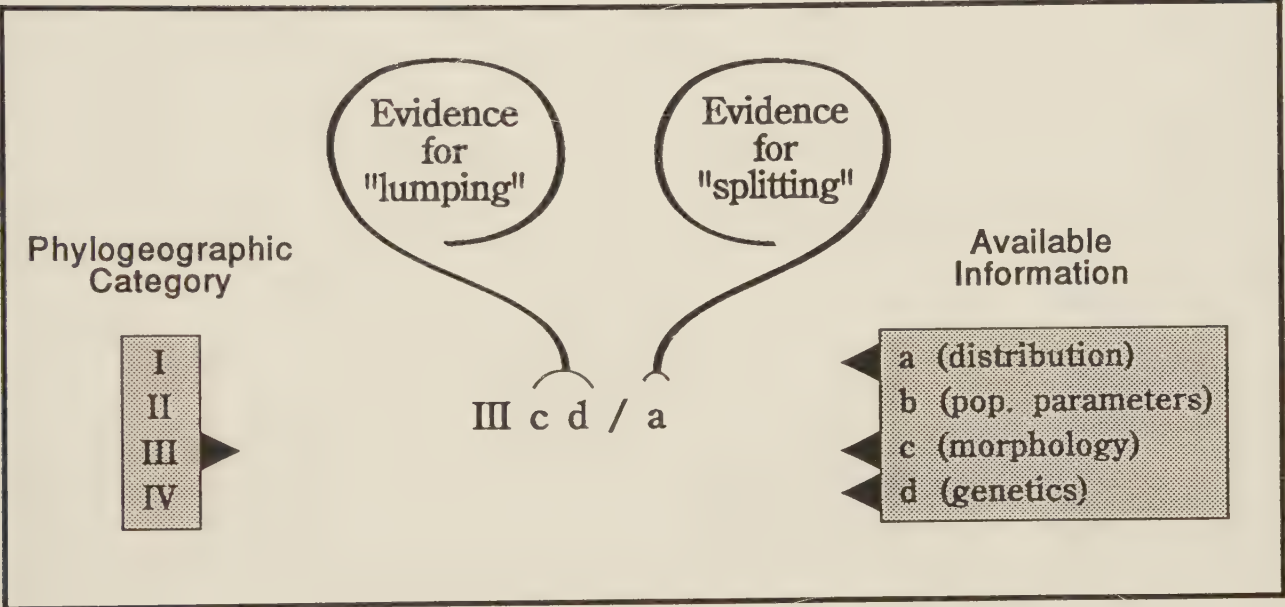
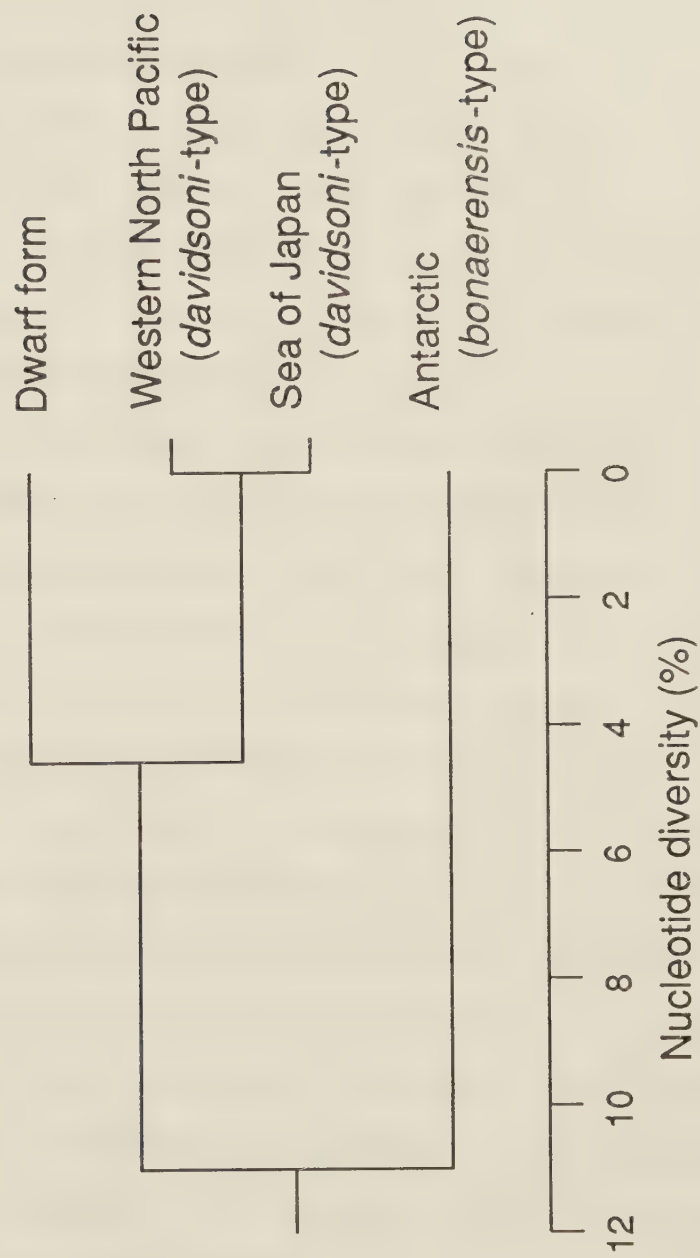


Fig. 4. mtDNA sequence divergence among four minke whale samples. After Numachi et al. 1989.



APPENDIX

In the earlier part of this paper, we have endeavored to show how stocks may be classified, with the aid of some guidelines, into one of four major categories. Information which describes characteristics of populations may then be added as qualifiers to include (a) distribution, (b) population response (demographic parameters), (c) phenotypic (morphologic), and (d) genotypic information (Fig. 3). Arguments for classification must be made in the knowledge that information is constantly being updated, and that intra-specific populations are dynamic and therefore subject to change themselves over time as well as information being newly discovered and reported. Our attempts at classifications are thus open to testing both now and in the future.

We have chosen the minke whale as our test case to illustrate our procedure. It has been comparatively well investigated so a great variety of information is available with which to make stock definitions. For completeness, we have endeavored to include a fairly detailed review of the now available and relevant literature regarding the species. We have organized the material in such a way that could serve as a model for future attempts at formal stock definitions.

MINKE WHALE

Balaenoptera acutorostrata

I. Taxonomy

A. Subspecies - bonaerensis

B. Morphs

1. Davidsoni-type
2. Bonaerensis-type
3. Dwarf

II. Provisional management units³

A. Southern Hemisphere - six management areas, defined by longitude from the equator to ice edge

1. Area I, 120°W-60°W
2. Area II, 60°W-0°
3. Area III, 0°-70°E
4. Area IV, 70°E-130°E
5. Area V, 130°E-170°W
6. Area VI, 170°W-120°W

B. Northern Hemisphere - two main populations, one smaller

1. North Atlantic

- a. Canadian east coast
- b. Central
- c. West Greenland

³ Populations and stocks as defined by the IWC - International Convention for the Regulation of Whaling, 1946, Schedule October 1989.

d. Northeastern

2. North Pacific

a. Okhotsk Sea - Western Pacific

b. Sea of Japan - Yellow Sea / East China Sea

c. East Okhotsk Sea - Western Pacific

3. Northern Indian Ocean

III. Evidence

A. Distribution

1. Range

Distribution is global, but there is no evidence from tagging, abundance, etc. that Northern and Southern Hemisphere populations mingle at any time, even though the equator may be breached in some regions, e.g., off Brazil. The pattern of latitudinal seasonal migration associated with feeding (in polar waters) and breeding (in warm low latitudes) effectively isolates the populations of the two hemispheres, by being out-of-phase by 6 months. However, there is still a possibility, yet to be proved, for interchange in some marginal equatorial regions where temporarily segregated portions of the population, e.g., mature females or males, may reside almost year-round. Latitudinal segregation of different portions of the population by sex, age, and reproductive status are well documented (Wada 1989).

Tag return data suggest mixing longitudinally at the boundaries (as defined above) between southern stocks (Wada

1984). There is evidence for interchange between Areas IV and V, for example. The region of occupation of the dwarf form in the southern oceans is longitudinally wide (Southwest and Southeast Atlantic, Southwest Pacific), but perhaps excluded from high latitudes (Best 1985; Arnold et al. 1987).

In the Northern Hemisphere, stocks have been defined mainly in response to national and regional exploitation patterns, and to a large extent were originally not biologically based; although tag experiments do not link West Greenland animals with the eastern Atlantic ones, they appear to be separate. Because the species is highly migratory, and movements of several thousands of kilometers, even within a few days, are well-documented in latitudinal direction (Horwood 1990), unless there are actual or partial geographic/oceanographic or other barriers to east-west excursions, the whales from the various regions must be considered probably to intermingle.

The relationship of the minke whales in the southern and northern Indian Ocean is not known, although populations exist on each side of the equator. The southern animals clearly relate to the Areas III and IV. In the northern region, animals are observed year-round in the Red Sea, Gulf of Aden, Persian Gulf, Sri Lanka and Indonesia (Horwood 1990).

2. Contaminants

Tanabe et al. (1986) reported concentrations of PCBs (0.0031-0.029 ppm wet weight) and DDEs (0.013-0.14 ppm wet weight) in blubber of Antarctic Area IV and V minke whales to be mostly lower than those observed for the Northern Hemisphere, where levels are 0.14-1.1 ppm wet weight for PCBs and 0.21-2.6 ppm DDT off West Greenland (Johansen et al. 1980), and 27.45 ppm PCBs and 1.09 ppm DDT in the St. Lawrence estuary, Canada (Sergeant 1980). The differences are clearly due to feeding ground separation, and show clear distinction between the Hemispheres.

3. Parasites

Comparison of infestation rates of ectoparasites in adjacent Antarctic Areas I, II, and III (Bushuev 1986, 1988) suggest differences, with 34-57% of the whales infested in Area III, 2-11% in Area II (with variable incidence from east to west), and almost zero infestation in Area I. Ohsumi et al. (1970) reported very low ectoparasite infestation in Area IV, and later investigation over 3 years showed significant differences between Areas I, III, and IV. The differences were interpreted as indicating separation of stocks on the feeding grounds.

B. Population response

The Southern Hemisphere minke whales have been documented to respond indirectly to exploitation of competitor species in

a density dependent manner, with consequential reduction in the age at sexual maturation from about 12-13yr to 7-8yr during a 30-year period (Area III) (Kato 1987). Masaki (1978, 1979), Kato (1983), Kato et al. (1984) and Ohsumi (1986) reported similar changes in age at sexual maturation for Areas III and IV combined. The pattern of trends and values of biological parameters seems similar for these Areas of the Southern Hemisphere, but perhaps the response has been greatest in the most heavily exploited Areas I, II, and III (Horwood 1990).

Rather less is known for the Northern Hemisphere because of difficulties in age determination. Still, sexual maturation is reported to be about 7.3yr in the North Atlantic.

C. Phenotypic Data

The Northern and Southern Hemisphere forms of the minke whale are different in coloration (flippers, baleen, etc.) size and skeletal morphology, the southern form being designated as the bonaerensis form. With the exception of the newly described dwarf form, mature animals from the southern population are generally larger than those from the northern populations (Lockyer 1984). The Atlantic minke is also slightly larger than the Pacific minke.

In the Southern Hemisphere, there are traditionally two morphological types reported, one with plain pigmented flippers and the other with asymmetrical two-tone coloration;

both belong to the bonaerensis forms (Williamson 1959; Ohsumi et al. 1970; Taylor 1957; Aguayo 1974; Baker 1983; Gaskin 1972; Kasuya & Ichihara 1965). Currently, there are three reported color forms of minke whale, mainly focused on extent and symmetry (left and right sides) of flipper coloration - the presence, absence or intermediary of a white band, the extent of pale coloration of the baleen, and dark pigmentation around the neck/throat region (Best 1985). The new evidence for a diminutive or dwarf form in the southern oceans, mainly reported from South Africa, Australia, New Zealand and Brazil (Best 1985), is largely based on the definition of this additional color morph that is characterized by symmetry of coloration and white flippers. In addition, the third form is consistently smaller, and has been described as a diminutive or dwarf form. Best (1985) concluded that the dwarf form was also sufficiently different in skull characters from the southern bonaerensis subspecies that it was at least as distinct as the northern davidsoni form from the bonaerensis one.

D. Genotypic Data

Restriction fragment analyses using 14 restriction enzymes on minke whale mtDNA D-loop from four populations, Antarctic Areas IV and V, bonaerensis type, Antarctic Area IV dwarf form, Sea of Japan and western North Pacific (davidsoni type), indicated 4-11% genetic nucleotide diversity between

them (Numachi et al. 1989). The genetic diversity within populations in Areas IV and V (bonaerensis form), is only 0.17%, 0.05% within western North Pacific and none within Sea of Japan. The nucleotide diversity shows no significant differences between Areas IV and V, but significant differences between bonaerensis, dwarf, and davidsoni forms, the latter two being relatively more closely related, with genetic diversity of about 4% (Fig. 4).

The diversity between the Sea of Japan and the western North Pacific is only 0.06%, but is >10% between Northern and Southern Hemisphere minke populations. Wada and Numachi (1989) presented results of enzyme electrophoresis on tissue proteins from different balaenopterid whales, which indicated genetic differentiation between Antarctic and western North Pacific Sea of Japan and Korean stocks was about seven times greater ($D = 0.0826$) than that within the North Pacific, to the extent that the differences were far greater than those between the separate sibling species B. borealis (sei) and B. bryde (Bryde's). This suggested separate species, or at least subspecies between northern and southern minke.

DNA nuclear probes suggest significant differences between the Antarctic, North Atlantic (West Greenland) and the western North Pacific (Sea of Japan) (Amos & Dover 1989). The results could be translated into migration rates between regions. The high level of migration between adjacent Areas IV

and V was enough to make separate stock identity questionable (Hoelzel & Dover 1989b).

In the North Atlantic, Palsboll (1990) reported on restriction fragment analysis of ribosomal DNA from minke from Northeastern Atlantic (Barents Sea) and West Greenland. He found that there was a probability of less than 0.001 that the two stocks were from a single random mating population, indicating good reasons for separate stock identity. Arnason and Spilliaert (1990) reported evidence for stock differences between minke from the Norway (Northeastern stock - Barents Sea), Iceland (Central stock) and West Greenland stock. Using genomic DNA probes, they found greatest differences between West Greenland and the others. There were also differences between Iceland and Barents Sea. They concluded that existing management stock divisions were valid. Danielsdottir et al. (1990) also found supporting evidence using electrophoretic analyses on the separation of these three stocks. Yet, using restriction fragment analysis of mtDNA, Palsboll (1990) found conflicting and contradictory results for these three regions. Bakke and El-Gewely (1990) reported stock differences between northern Norway and west coast of Svalbard using the same techniques.

IV. Classification

The minke whale represents a species that has been comparatively well investigated and defined in terms of stock

identity. Because the species has been exploited on an international scale, this has probably been the reason for this knowledge being forthcoming. It seems well evidenced that the Northern and Southern Hemisphere populations are clearly distinct and in category Ib/abcd status, and the subspecies category seems valid. The North Atlantic versus North Pacific also appear distinct and in category I status.

In the Southern Hemisphere, clearly it seems that Areas III, IV, and V are not easily discernable and probably should be afforded category IVabcd/a status - very weak stock definition, if at all. However, comparing the dwarf form with the southern bonaerensis subspecies, the diminutive form also could be afforded subspecies status, but be ascribed to the category II because of sympatric distribution. The final categorization might be IIa/cd.

The North Atlantic stock definitions appear largely to be supported by genetic analyses, and the majority when compared would be afforded category IIIc/acd status.

This species is of particular interest in stock analysis because of multiple representations in each stock category I-IV. The recent genetic investigations have brought to light the fact that speciation, not just subspeciation, is and has been occurring in the minke whale populations, relative to other species (namely sei and Bryde's). In the future, the

whole question of what constitutes a species may have to be reconsidered for the family Balaenopteridae.

